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Modelling mechanisms of social network maintenance in hunter–gatherers

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ABSTRACT

Due to decreasing resource densities, higher latitude hunter–gatherers need to maintain their social networks over greater geographic distances than their equatorial counterparts. This suggests that as latitude increases, the frequency of face-to-face interaction decreases for 'weak tie' relationships in the outer mating pool (~500-strong) and tribal (~1500-strong) layers of a hunter-gatherer social network. A key question, then, is how a hunter-gatherer tribe sustains coherence as a single identifiable unit given that members are distributed across a large geographic area. The first step in answering this question is to establish whether the expectation that network maintenance raises a challenge for hunter–gatherers is correct, or whether sustaining inter-group contact is in fact trivial. Here I present a null model that represents mobile groups as randomly and independently moving gas particles. The aim of this model is to examine whether face-to-face contact can be maintained with every member of an individual's tribe at all latitudes even under the baseline assumption of random movement. Contrary to baseline expectations, the number of encounters between groups predicted by the gas model cannot support tribal cohesion and is significantly negatively associated with absolute latitude. In addition, above ~40° latitude random mobility no longer produces a sufficient number of encounters between groups to maintain contact across the 500-strong mating pool. These model predictions suggest that the outermost layers of hunter–gatherers' social networks may require additional mechanisms of support in the form of strategies that either enhance encounter rates, such as coordinated mobility patterns, or lessen the need for face-to-face interaction, such as the use of symbolic artefacts to represent social affiliations. Given the predicted decline in encounters away from the equator, such additional supports might be most strongly expressed at high latitudes.

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1. Introduction

Modern human social networks comprise a series of concentric layers that decrease in intimacy as they expand out from each individual (Roberts, 2010; Roberts et al., 2009). These layers appear to map onto ethnographically observed groupings that recur in archaeological (e.g. Grove, 2010b, 2011) and anthropological studies (e.g. Hamilton et al., 2007; Zhou et al., 2005), suggesting that they may be universal features of human social organisation. There is compelling evidence that the size of an individual's social network and the quality of their supportive social relationships are positively related to their life-expectancy (Holt-Lunstad et al., 2010; Kroenke et al., 2006; Pinquart and Duberstein, 2010), their mental and physical health (e.g. Umberson and Montez, 2010), and the health and survival of their children (Adams et al., 2002; Iaupuni et al., 2005). Maintaining one's social network is therefore crucial for survival and reproduction.

Extensive social networks facilitate the spread of information, knowledge and resources. At the lowest level, independent family units nested within bands pool risk associated with foraging by sharing unpredictable resources such as meat (Hames, 1990; Kaplan et al., 1990; Winterhalder, 1996). If the environment is sufficiently heterogeneous for scarcity in one region to parallel abundance in another, exchange of information and resources may occur between residential bands. At the highest level, such exchange may occur across the entire mating pool (~500 individuals in an endogamous 'megaband' comprising a number of residential bands) and ethnolinguistic tribe (~1500 individuals comprising several mating pools) (Dunbar, 1998; Zhou et al., 2005). The mating pool and tribe are the outermost network layers beyond each individual's 'active network' of people that they feel they share a relationship with and with whom they make a conscious effort to

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keep in contact (Roberts, 2010). Keeping track of the indirect or 'weak' ties that emerge from the overlapping active networks within a tribe allows individuals access to a wider variety of resources and information covering a greater geographic area through 'friends of friends'.

Since resource seasonality generally increases and resource density generally decreases with latitude (Grove et al., 2012; Nettle, 1999), nearer the poles it might become particularly imperative for hunter–gatherers to be able to (i) ensure safe passage during the seasonal round by avoiding conflict with the members of different residential groups, (ii) share information about the whereabouts of resources and (iii) conserve cultural knowledge about storage processes and the manufacture of reliable and diverse technology through social learning. Given that these functions are principally facilitated through social relationships, large cohesive social networks might be especially important for high latitude hunter-gatherers (Pearce et al., 2014). However, although social bonds can help assuage ecological difficulties, the maintenance of social networks is likely to present cognitive challenges in terms of coordination of individuals or sub-groups and time management challenges in relation to ensuring sufficient time investment in face-to-face bonding, without which relationships tend to deteriorate (Roberts and Dunbar, 2011; Sutcliffe et al., 2011). These challenges are likely to be exacerbated at higher latitudes for at least two reasons. Firstly, since the geographic area occupied by each population (tribe) increases faster with absolute latitude than does the size of the population (tribe) itself, social networks become spread over greater home ranges at higher latitudes: see Fig. 1 (Grove et al., 2012; Kelly, 1995; Pearce et al., 2014). Maintaining relationships across long distances is costly in terms of time and the risk of exploitation (Fitzhugh et al., 2011). Secondly, as larger groupings fission into smaller, more numerous foraging units in order to maintain manageable day journey lengths at higher latitudes, individuals need to mentally keep track of, and coordinate, larger numbers of groups (Grove et al., 2012; Lehmann et al., 2007).

If high latitude individuals are to reap the benefits of extensive social networks, they require the means to sustain social bonds with partners in different groups dispersed over wide areas. Travelling to visit more distant groups or to take part in periodic aggregations is likely to be time-costly. However, one way of absorbing these potential time costs is to embed social activities within more subsistence-based ones (Whallon and Lovis, 2011). Mobility primarily linked to tracking resources might allow hunter-gatherers to remain connected through coincidental encounters with neighbouring groups. Higher latitude groups tend to exhibit higher mobility that their lower latitude counterparts (Fig. 2) and this may allow sufficient inter-group encounters to counteract the distribution of social networks across larger home range areas at high latitudes. An important question, then, is whether the normal movement of groups around the landscape for resource gathering could inadvertently allow neighbouring groups to stay connected without having to resort to special social visiting trips or other mechanisms of contact and cohesion that allow social ties to remain active in the absence of frequent face-to-face contact, such as the exchange of symbolic artefacts.

Hunter–gatherer mobility patterns vary both between different populations and seasonally over a year (Bettinger, 1999; Binford, 1980; Watanabe, 1968). However, in general, foraging subgroups from the same residential band tend to move radially out from, and back to, a home base, which is moved periodically within a home range when local resources are depleted and according to seasonal changes in resource distributions (Kelly, 1995). Foraging groups may return to their home base nightly, or may conduct more extended logistic trips to procure particular resources (Binford, 1980). The size of the residential band occupying a particular home base may vary according to season and bands may periodically fuse with other bands to form larger aggregations at particular locations where resources are relatively plentiful (Binford, 2001). Whether nightly coordination between band members and seasonal coordination between bands are consciously determined or merely a side-effect of resource distributions dictating aggregation

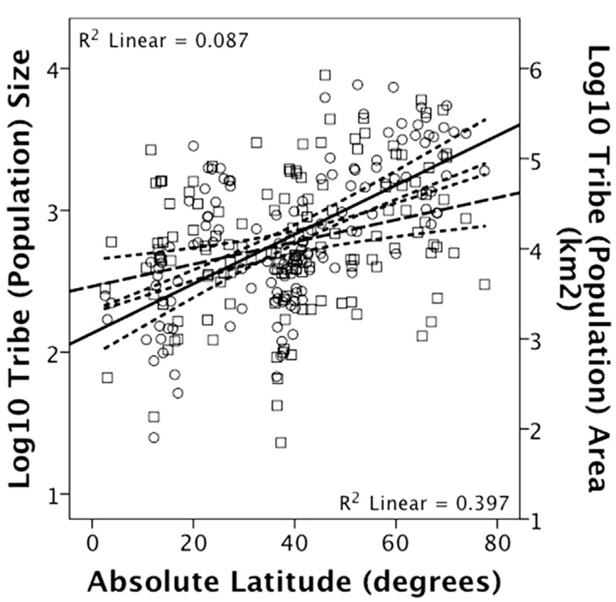

Fig. 1. Log_{10} total ethnic population/tribe (squares, long-dashed line) and $\log_{10}$ total home range area associated with the total ethnic population/tribe (circles, solid line) of each society plotted against absolute latitude for 136 hunter–gatherer societies (Binford, 2001). The short-dashed lines indicate 95% confidence limits for the regression lines. Note that the home range area associated with each tribe/population increases at a greater rate with absolute latitude (the slope is steeper) than does tribe/population size.

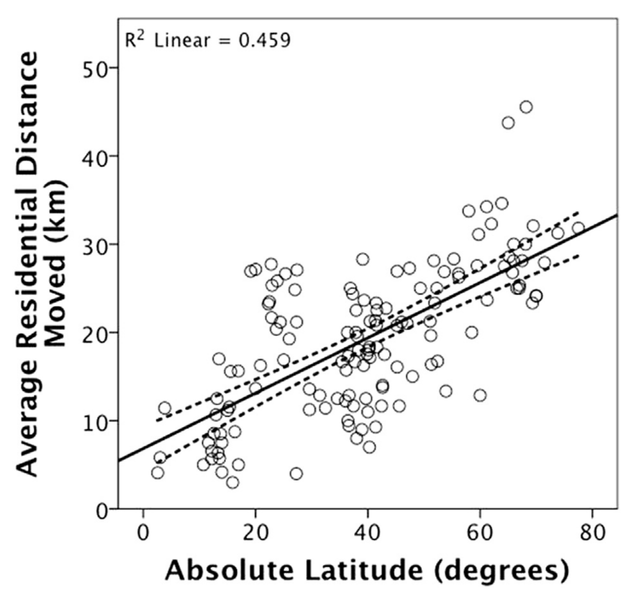

Fig. 2. The average distance covered per residential move (the total distance moved in a year divided by the number of residential moves in a year) plotted against absolute latitude for 136 hunter–gatherer societies (Binford, 2001). The dashed lines indicate 95% confidence limits for the regression line.

points, such mobility patterns ensure that groups meet each other, thus providing the opportunity for social ties to be maintained through face-to-face interaction.

Due to the factors listed above, namely dispersion over a larger home range area and fissioning into greater numbers of subunits, there is reason to suppose that high latitude hunter-gatherers should have more difficulty maintaining their social networks than their equatorial counterparts. However, before attempting to identify possible solutions to this apparent problem, we need to know that the problem exists in the first place. In this paper I investigate whether or not it is trivial for hunter-gatherers to maintain their social networks. To do so I present a null model that gives the worst case scenario in terms of encounter rates: I test whether or not hunter-gatherer groups would bump into a sufficient number of other groups to enable them to maintain face-to-face contact with all members of their active network (~150 individuals), mating pool (~500 individuals) and tribe (~1500 individuals), even if they were moving randomly around their tribal home range rather than being coordinated in any way. In other words, the null model predicts whether sufficient encounters occur even without behavioural strategies (such as coordination and habitat-structured mobility) or cultural mechanisms (such as exchange of symbolic artefacts or linguistic markers of affiliation) that would, respectively, elevate encounter rates or reduce the required frequency for face-to-face interaction in order to maintain social bonds. If this null model fails to predict adequate numbers of encounters in certain environments, future modelling work can build upon this baseline model to understand which factors, such as the existence of base camps or seasonally clustered resources, might contribute to network maintenance in those habitats. Although empirical data to validate these models is so far lacking, recent network analysis work with the Hadza (Apicella et al., 2012) suggests that fieldworkers may soon be able to provide the necessary quantitative information on hunter-gatherer interaction patterns to test the model predictions. In the meantime, the null model outlined in this paper is a crucial first step in elucidating whether network maintenance presents a difficulty for hunter-gatherers in certain environments or whether even random mobility allows tribal cohesion through coincidental meetings between independently moving groups.

In order to investigate whether mobility inadvertently allows tribal members to remain connected with each other even under the null assumption of random movement, I use a gas modelling approach borrowed from the physical sciences. The ideal gas model equation links the number of times gas particles come within a specified distance of each other to their density and speed, as they move randomly and independently within a two-dimensional space (Grove, 2010a; Grove et al., 2012; Hutchinson and Waser, 2007): Fig. 3. Gas models have previously been used extensively in biology (Hutchinson and Waser, 2007), including in non-human primate behavioural ecology to study mating systems (e.g. in callitrichids: reviewed in Dunbar, 2002; in gorillas: Harcourt and Greenberg, 2001), territory defense (across non-human primates: Lowen and Dunbar, 1994) and intergroup encounters (in grey-cheeked mangabeys: Barrett and Lowen, 1998). More recently, gas models have been used to look at hunter-gatherer foraging and mobility strategies (Grove, 2010a) and hominin fission-fusion dynamics (Grove et al., 2012). To my knowledge the gas model presented here represents the first application of this method to addressing questions of social network cohesion in hunter-gatherers. The gas model provides a novel approach to hunter-gatherer sociality by looking at whether chance meetings between mobile groups can act as a mechanism of social cohesion in different environments, even under random mobility.

As Fig. 3 demonstrates, in the hunter-gatherer gas model mobile groups (family units or residential bands) are taken to be analogous to gas particles moving around their tribal home range. When applied to hunter–gatherer behaviour, the gas model predicts the

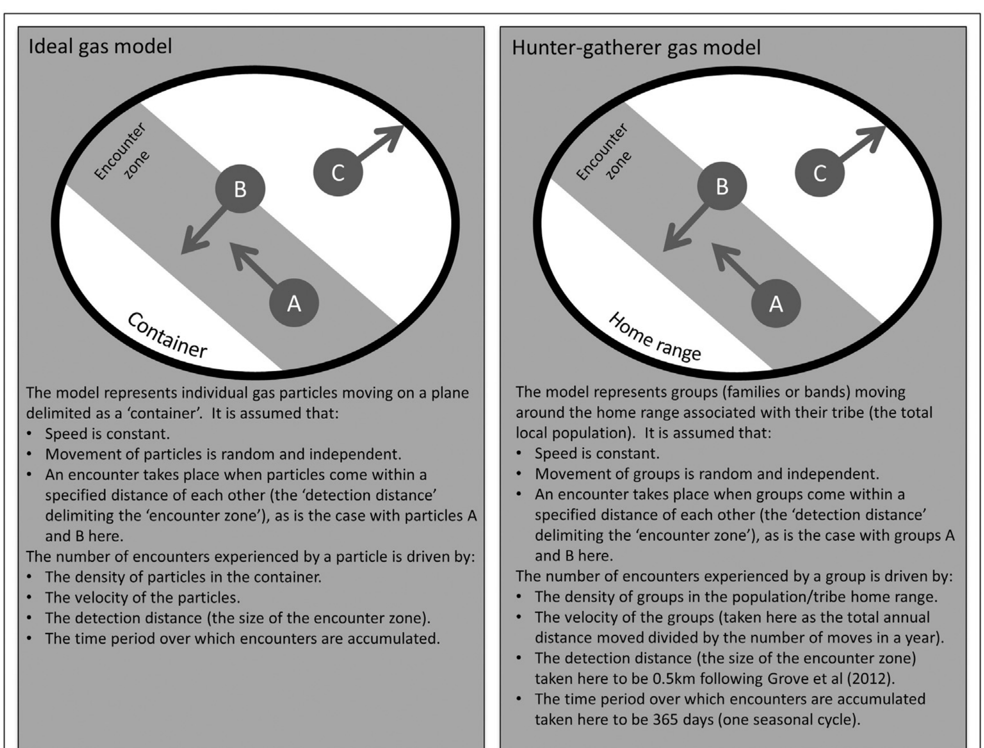

Fig. 3. Schematic comparing the ideal gas model (left) and its application in this paper to hunter–gatherer social networks (right).

number of times a group of a particular size ‘encounters’ (that is, comes within a specified distance and is thus aware of) another group. I model groups at varying degrees of fission-fusion: (i) families, (ii) residential bands in the most dispersed phase of the seasonal cycle and (iii) residential bands in the most aggregated phase of the seasonal cycle. It is assumed that if groups detect each other, they will interact, thus sustaining social ties between all individuals in both groups.

An encounter between groups is taken to provide an opportunity for social ties to be created or reinforced between their individual members. Since we know the average number of individuals in each nested layer of social organization (the family, foraging party/dispersed band, aggregated band, mating pool and tribe) from ethnographic data (e.g. Hamilton et al., 2007; Zhou et al., 2005), through predicting the number of encounters between groups, the hunter-gatherer gas model allows us to ascertain whether the predicted number of encounters at least equals the number of individuals in a specified layer of an average social network. If the number of encounters predicted by the gas model is above this threshold, this would indicate that all the relationships in that layer could be maintained through face-to-face contact. I assume that all moving groups belong to the same ethnolinguistic tribe and that the tribe is the maximum size of network that needs to be maintained as an integrated, identifiable unit.

The gas model simulates the movement of groups (aggregations of individuals) and estimates the number of interactions between groups, rather than modelling the precise structure of the network of relationships between individuals and groups. Nonetheless the gas model is applicable to modelling the maintenance of social networks because it predicts the number of opportunities available for social tie formation through face-to-face contact: maintenance requires interaction between groups, during which the individuals within each group can bond with each member of the other group. Even if the exact structure of the interactions is not made explicit by the gas modelling approach, the predicted number of encounters acts as a proxy for the number of individuals (nodes) maintained within a network through face-to-face ties (edges). In other words, the gas model indicates the total number of ties that could be maintained in the network of an average group member.

Groups will not encounter each other if their density is too low or if their velocity is too low. For instance, at high latitudes there may be too few groups in a large tribal home range and groups may not travel far enough each day for their paths to cross. The problem of gaining sufficient encounters with other groups will be exacerbated if the detection distance is very small, for instance if groups cannot see each other until they physically encounter each other due to dense foliage. In the hunter-gatherer gas model presented here, the detection distance is held constant, so the factors that determine whether sufficient encounters will occur between mobile hunter-gatherer families or bands are the density of groups (driven by tribal home range area and group size) and the distance groups move each day. Since both population density and the total annual distance moved by bands are significantly related to the degree to which societies depend on hunting (Grove, 2010a), the number of encounters for a particular society, being driven by group density and mobility, may be influenced by the percentage of the diet comprising hunted terrestrial animals. Consequently, in addition to the effect of absolute latitude on encounter rates, I examine the influence of the proportion of the diet that relies on hunting in different hunter-gatherer populations.

Using the gas model I test the hypotheses that (i) maintaining social networks is trivial: there are sufficient numbers of encounters annually in order to maintain face-to-face ties with all members of all social network layers up to and including the 1500-strong tribe even when movement is random, (ii) the predicted number of encounters remains constant across latitude, meaning that network maintenance is trivial in all environments, because although the density of groups decreases with increasing latitude, this is counterbalanced by increased mobility nearer the poles and (iii) variation in the number of encounters predicted by the gas model for each latitude is partly explained by differences in the contribution of hunting to the diet in different societies. Rejection of the first two hypotheses would provide the impetus for future models exploring factors that promote interaction between mobile groups.

In order to test these hypotheses I present the following analyses: first, linear models regressing the predicted number of encounters for all societies on absolute latitude and the percentage contribution of hunting to the diet and second, comparisons of the average number of encounters predicted for North American hunter-gatherers between high and low latitude biomes. I concentrate on North America because this area provides the largest sample of hunter-gatherer societies. If the predicted number of encounters would allow contact with at least 1500 individuals (the exact number of encounters required will depend on the size of the mobile subgroup being modelled) at all latitudes and for all biomes, this would suggest that even random movement could allow face-to-face contact to be maintained between all members of the average tribe. In turn this would imply that, contrary to expectation, maintaining tribal cohesion is trivial for hunter-gatherers even at high latitudes. In contrast, if numbers of encounters become insufficient above a particular latitude or in a particular biome, this would identify a possible a breakpoint where network maintenance is no longer trivial for a specific network layer. If random mobility fails to ensure sufficient face-to-face interaction, this paves the way for future work examining the factors that do.

2. Material & methods

The ideal gas model is used as a heuristic device to model human interaction between mobile groups. I model human interaction by using ethnographic correlates of the original gas model parameters, which are characterised below (see also Fig. 3). In this Section I outline the ethnographic data used, the different social network layers modelled and the structure of the hunter-gatherer gas model.

2.1. Ethnographic data

I use hunter–gatherer home range area, mobility and group size data from Binford (2001), excluding mounted, ‘suspect’ and sedentary societies. Forty-two of the hunter–gatherer societies did not have mobility data, leaving a sample of 136 societies in the dataset. Table 1 illustrates the mobility, group size and area data used in the gas model.

Binford gives group size data for multiple layers of social organization: family, dispersed band (Binford's Group 1: the size of the residential band during seasons of dispersion), aggregated band (Binford's Group 2: the size of the residential band during seasons of aggregation), periodic aggregations of bands forming the mating pool (Binford's Group 3) and ethnolinguistic tribe (Binford's Population). Here I present gas model outputs for the first three layers only (family, dispersed band and aggregated band) because the larger groupings do not move together as integrated units.

From the group size and area data I calculated the number of each type of sub-group in the total ethnolinguistic tribe (Population) and the density of these different types of sub-groups in the tribal home range area (the total area associated with the Population). The mobility data provided by Binford are the total distance

Table 1
Descriptive statistics (median, minimum, maximum) for the ethnographic group size, area, and mobility data used in the gas model for each biome and the subsistence data used in statistical analysis (data from Binford, 2001). The North American biomes are shaded and in bold. N = Number of societies.

Biome		Absolute latitude (degrees)	Hunting (% of subsistence)	Size of: Family	Band: Dispersed	Band: Aggregated	Tribe	Tribal area (km^2)	Average residential move distance (km)
(Sub)tropical Asia	*N*	4	4	2	4	4	4	4	4
	Median	13	28	3	11	34	4289	1185	6
	Min.	11	20	3	9	23	255	570	5
	Max.	52	65	4	20	60	3200	74,400	23
(Sub)tropical South America	*N*	5	5	3	5	5	5	5	5
	Median	46	40	4	19	45	2500	8800	12
	Min.	3	11	4	13	24	66	1640	4
	Max.	60	75	5	25	75	9000	475,300	21
(Sub)tropical Africa	*N*	6	6	3	5	6	6	6	6
	Median	21	43	5	10	30	446	11,400	20
	Min.	4	33	3	6	21	122	2500	11
	Max.	2	48	5	17	54	726	57,000	27
Australia (all biomes)	*N*	35	35	16	31	28	35	35	35
	Median	20	25	6	11	32	572	7200	13
	Min.	12	5	4	7	21	35	80	3
	Max.	43	45	8	20	60	2662	137,800	28
California & Northern Mexico	***N***	**15**	**15**	**2**	**7**	**13**	**15**	**15**	**15**
	Median	**38**	**25**	**5**	**17**	**40**	**1000**	**5800**	**12**
	Min.	**30**	**10**	**4**	**10**	**21**	**92**	**380**	**7**
	Max.	**43**	**40**	**6**	**19**	**62**	**3000**	**16,600**	**21**
North America	***N***	**27**	**27**	**2**	**22**	**22**	**27**	**27**	**27**
Desert & Desert Scrub	**Median**	**39**	**40**	**4**	**11**	**30**	**385**	**5260**	**18**
	Min.	**25**	**15**	**4**	**8**	**20**	**23**	**650**	**11**
	Max.	**45**	**55**	**4**	**21**	**55**	**1877**	**33,760**	**28**
Subarctic	***N***	**29**	**29**	**13**	**26**	**28**	**29**	**29**	**29**
	Median	**56**	**60**	**4.**	**17**	**53**	**1000**	**96,000**	**26**
	Min.	**45**	**20**	**3**	**6**	**25**	**185**	**5400**	**12**
	Max.	**74**	**75**	**7**	**32**	**95**	**4863**	**660,000**	**35**
Arctic	***N***	**15**	**15**	**11**	**15**	**15**	**15**	**15**	**15**
	Median	**67**	**30**	**5**	**18**	**35**	**550**	**52,500**	**29**
	Min.	**55**	**5**	**3**	**11**	**25**	**130**	**18,700**	**23**
	Max.	**77**	**89**	**6**	**22**	**85**	**6000**	**370,600**	**45**

moved per year between the location of different base camps (i.e. residential mobility) and the number of residential moves made in a year. From these the average distance traversed per move was calculated and used as a proxy for variation in daily velocity across different societies.

2.2. Social network layers

I present the modelled number of encounters for both the family and the residential band at two different degrees of fission-fusion (Binford's Group 1 dispersed band and Group 2 aggregated band) units. Although increased fissioning into smaller family units should increase the encounter rate due to the higher density of groups, the required number of encounters with other groups in order to maintain the same sized social network overall would also increase. Modelling the numbers of encounters at these three grouping layers tests whether the theoretical increase in the number of encounters associated with fissioning allows the same sized, or larger, network to remain connected under the null assumption of random mobility.

As mentioned in the Introduction, human social networks comprise a series of nested layers containing, on average, 5, 15, 50, 150, 500 and 1500 individuals (Zhou et al., 2005), see Table 2. For the purpose of the hunter–gatherer gas model, the family unit is taken to represent the ~5-individual level of the social network, so interaction frequencies between family units are seen to be at least at the 15-layer level (Table 2): three families interacting together create the 15-strong social network layer for individual members. For the purposes of the model, the ~5-strong ‘family’ unit could represent either (i) the basal unit of band social organisation i.e. the nuclear family or (ii) small foraging parties arising from division of labour. The dispersed band unit is assumed to represent the 15-layer, with interaction between units assumed to be at least at the 50-layer level (Table 2). The aggregated band unit is assumed to represent the 50-layer, meaning that interactions between band units are at least at the 150-layer level (Table 2).

The numbers of encounters for each hunter-gatherer society at each of these three grouping levels (family, dispersed band, aggregated band) are presented in Figs. 4 and 5. Superimposed on

Table 2
The number of encounters required for different network layers to be maintained through inter-personal contact for family and band units.

Social network layers	Binford's (2001) terminology	Number of encounters required for: A family unit	A dispersed band unit	An aggregated band unit
Family (5 individuals)	Family	0	0	0
Foraging Party or Dispersed Band (15 individuals)	Group 1	2	0	0
Aggregated Band (50 individuals)	Group 2	9	2	0
Active Network (150 individuals)	Group 3	29	9	2
Mating Pool (500 individuals)		99	29	9
Ethnolinguistic Tribe (1500 individuals)	Population	299	99	29

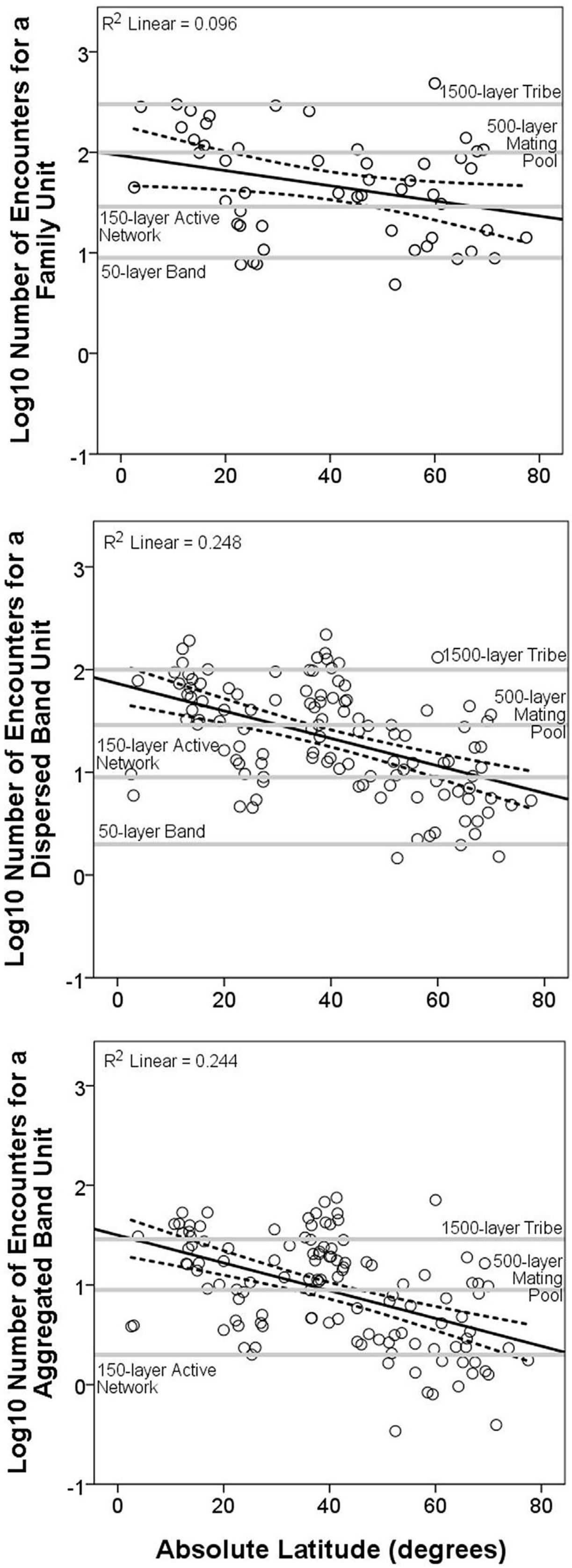

Fig. 4. Log_{10} number of encounters for a family (top), dispersed band (centre) and aggregated (bottom) band predicted by the gas model plotted against absolute latitude. The dashed lines indicate 95% confidence limits for the regression line. The superimposed horizontal grey lines are reference lines representing the number of encounters required in order to maintain face-to-face contact between all members of the band (50-layer), active network (150-layer), mating pool (500-layer) and tribal (1500-layer) social network layers.

these figures are reference thresholds representing the number of encounters required to maintain face-to-face contact with all members of the active network, mating pool and tribal network layers, given the size of the basal mobile group (Table 2). These thresholds are the total number of social units comprising a particular social network layer minus one: the focal group needs to maintain contact with *N-1* other groups, where *N* is the total number of subunits within a particular network layer based on ethnographic observations (Dunbar, 1998; Zhou et al., 2005): Table 2. For example, a family unit needs to maintain contact with 99 other 5-strong family units in order to retain membership of a 500-strong endogamous mating pool.

2.3. The hunter–gatherer gas model

The gas model equation predicts how frequently a focal group encounters another group within a particular area. In the model presented here, groups move across the entire home range of their ethnolinguistic tribe (Binford's (2001) 'Population' grouping). For both the family and band grouping levels I calculated the number of encounters between like-groups: a family unit encountering another family unit and a band unit encountering another band unit. All calculations were run using code written in *R*.

Hutchinson & Waser's (2007) equation for calculating the daily rate of encounter was converted into an equation that calculates the number of encounters, *E*, within a specified time period by multiplying the numerator by time *t*, yielding the equation:

$$E = \frac{8\rho D v t}{\pi}$$

t = time period
ρ = density of groups
D = detection distance
v = velocity

I limited t to 365 days to look at mobility within once seasonal round and here I present the total predicted number of encounters during one year. The density of groups was calculated as the number of family or band groups per population divided by the total population area. Velocity was calculated as the total distance moved in a year divided by the total number of moves within a year (data from Binford, 2001). This estimation of v gives the average distance moved per residential move (assumed to be achieved in a single day: *velocity* = *distance/1 day*) rather than the daily distance travelled specifically for foraging purposes. Nonetheless, average residential distance gives a proxy for increased mobility with latitude and agrees fairly well with actual foraging ranges (distance from base camp, which should be doubled to give total distance moved to and from camp each day, assuming that hunter-gatherers avoid redundancy: Grove et al., 2012): actual foraging ranges of 6–25 km, giving total distances travelled of 12–50 km (Layton et al., 2012), compared to estimated average residential distances of 3–45 km (*median* = 20 km) (data from Binford, 2001). When velocity was held constant across all societies at 25 km/day or 40 km/day (Grove et al., 2012; Layton et al., 2012) similar results were obtained as those presented here.

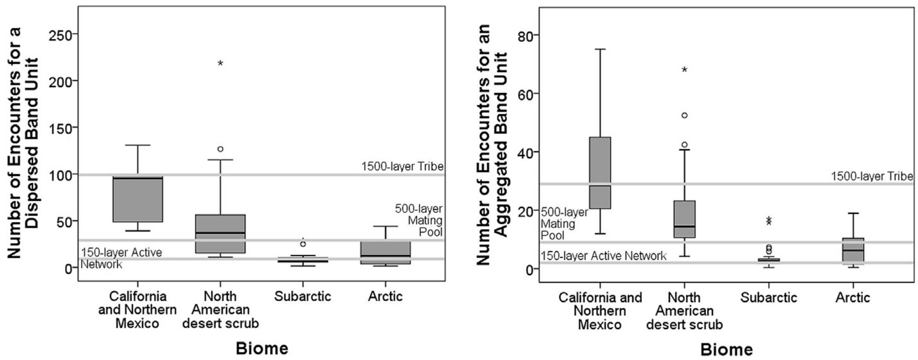

Fig. 5. Boxplots showing the number of encounters predicted by the gas model for the four North American biomes for a dispersed band (left) and aggregated band (right). The horizontal line shows the median, the box shows the interquartile range and the whiskers show the minimum and maximum, with outliers identified by points. The superimposed horizontal grey lines are reference lines representing the number of encounters required in order to maintain face-to-face contact between all members of the active network (150-layer), mating pool (500-layer) and tribal (1500-layer) social network layers.

'Detection distance' can be understood as the distance within which two groups need to come of one another in order for an 'encounter' to have taken place. If the diameter of a social group is s and the maximum detection distance between individuals is d (taken here to be 0.5 km, following Grove et al. (2012)), the individuals travelling at the periphery of the two groups may detect each other when the group centres are less than or equal to $d + s$ apart (the detection distance between the periphery of the group, d,

Table 3
The median, minimum and maximum number of encounters predicted for a family or dispersed/aggregated band during one year in each biome. Shading indicates that the predicted number of encounters exceeds the threshold required to remain connected with the members of an individual's active network of 150 individuals (light grey) and mating pool network of 500 individuals (dark grey).

Biome		Number of encounters predicted by the gas model during one year for:		
		A Family Unit	A Band	
			Dispersed	Aggregated
(Sub)tropical Asia	N	2	4	4
	Median	281	92	32
	Minimum	262	24	8
	Maximum	301	159	53
(Sub)tropical South America	N	3	5	5
	Median	45	10	4
	Minimum	37	6	3
	Maximum	487	132	71
(Sub)tropical Africa	N	3	5	6
	Median	110	40	9
	Minimum	83	9	2
	Maximum	284	78	31
Australia (all biomes)	N	16	31	28
	Median	29	40	17
	Minimum	8	5	2
	Maximum	231	192	53
California & Northern Mexico	N	2	7	13
	Median	275	95	28
	Minimum	258	39	12
	Maximum	292	131	75
North America Desert & Desert Scrub	N	2	22	22
	Median	61	37	14
	Minimum	39	11	4
	Maximum	82	219	68
Subarctic	N	13	26	28
	Median	31	7	3
	Minimum	5	1	0
	Maximum	107	29	17
Arctic	N	11	15	15
	Median	69	12	6
	Minimum	9	2	0
	Maximum	139	44	19

plus the radii of both groups, s) (Hutchinson and Waser, 2007). The detection distance D equates with $d + s$. Here, each person is assumed to take up a conservative 1 m diameter circle of space, the area of which was multiplied by total group size to give a total group-cluster area, from which the diameter s was calculated in kilometres. When each person was assumed to take up a 5 m diameter circle of space, the output of the gas models did not differ qualitatively from those presented here, even though increasing the group diameter increases the detection distance and therefore the predicted number of encounters. This suggests that the results are robust to small changes in parameter values.

The predicted number of encounters were $\log_{10}$-transformed in order to fit linear models. Given the lack of an adequate hunter-gatherer phylogeny to date I do not correct for possible lack of independence between societies due to shared history, but instead use standard Least Squares Regression models. The residuals of these regressions did not differ significantly from normal (Kolmogorov–Smirnov one-sample test with Lilliefors correction) and did not show heteroscedasticity.

3. Results

The total numbers of encounters in a year predicted by the gas model for each hunter-gatherer society are presented first regressed against absolute latitude (Fig. 4), initially alone and then controlling for the contribution of hunting to the diet, and then as comparisons between the average number of encounters in each biome, focussing on North America (Fig. 5, Table 3). Biome and absolute latitude are not included in the same statistical models because they are different ways of expressing the same variable, namely variation in resource distributions between the different environments inhabited by hunter-gatherers, and thus show high co-variance.

In both Figs. 4 and 5 reference lines are included to indicate whether sufficient encounters are reached in order to maintain face-to-face contact with each member of an averaged-sized active network, mating pool and tribe. The reference lines allow hypothesis (i), that network maintenance is trivial, to be tested. The linear regressions against absolute latitude test hypothesis (ii), that network maintenance remains trivial at all latitudes, to be tested. Including percentage hunting as a covariate allows exploration of possible reasons for variation in the predicted number of encounters at each latitude and tests hypothesis (iii), that contribution of hunting to the diet influences the number of encounters predicted.

3.1. Numbers of encounters and absolute latitude

Ordinary Least Square regressions revealed significant positive relationships between absolute latitude and the annual number of encounters predicted for all three grouping levels, Fig. 4: family ($t_{50} = -2.298$, $p = 0.026$, $R^2 = 0.096$), dispersed band ($t_{113} = -6.105$, $p < 0.0001$, $R^2 = 0.248$) and aggregated band ($t_{119} = -6.203$, $p < 0.0001$, $R^2 = 0.244$). The fitted regression lines in Fig. 4 suggest that in equatorial regions there may be sufficient numbers of encounters in order to sustain contact with all members of the tribe for aggregated band units only. Elsewhere it is predicted that face-to-face interaction arising from random movement would not allow the tribe to remain cohesive (the regression lines do not cross the reference line representing the tribe). For the more fissioned family and dispersed band units, tribal cohesion could not be maintained at any latitude. The fitted regression lines also indicate that above ~40° latitude, bands (both dispersed and aggregated) do not experience sufficient numbers of encounters through random movement to sustain contact across their mating pools. In contrast, randomly moving family units cannot sustain contact with all members of the mating pool at any latitude. Furthermore, the fitted regression lines in Fig. 4 suggest that between 65 and 80° latitude (depending on the size of the mobile unit in question) random movement may even fail to allow incidental interactions with all members of an individual's active network for family and dispersed band units.

3.2. The impact of foraging strategy on numbers of encounters

To explore the possible reasons for the variance in the number of encounters predicted for different societies inhabiting the same latitude, multiple linear regressions were run with both absolute latitude and the percentage of the diet procured through hunting as independent variables. For the dispersed and aggregated bands the significant negative relationship between absolute latitude and the annual number of encounters remained independently of the percentage of hunting in the subsistence base (dispersed band: % hunting $t_{112} = -3.388$, $p = 0.001$, absolute latitude $t_{112} = -3.526$, $p = 0.001$, overall adjusted $R^2 = 0.306$, aggregated band: %hunting $t_{118} = -3.691$, $p < 0.0001$, absolute latitude $t_{118} = -3.568$, $p = 0.001$ overall adjusted $R^2 = 0.311$). For mobile family units only percentage hunting showed a significant partial relationship with the annual number of encounters once the effects of absolute latitude were partialled out (%hunting: $t_{49} = -2.085$, $p = 0.042$, absolute latitude: $t_{49} = -1.223$, $p = 0.227$, overall adjusted $R^2 = 0.135$).

3.3. The number of encounters in different North American biomes

Fig. 5 presents the annual number of encounters for each of the four North American biomes for randomly moving band units (see Table 3 for all biomes). The predicted number of encounters for family units are not shown due to the small sample size for the lower latitude biomes, but are given in Table 3. The two lower latitude California/Northern Mexico and desert/desert scrub biomes have predicted numbers of encounters that would allow them to meet all members of their mating pool face-to-face during the year, whereas the gas model predicts that hunter-gatherers inhabiting the higher latitude subarctic and arctic biomes could only just manage to retain contact across their active network through random movement alone.

To test whether the gas model predicted significantly different numbers of encounters in the high and low latitude biomes, I statistically compared the average number of encounters predicted for the lower latitude California/Mexico and desert/desert scrub biomes with the average number of encounters predicted for the higher latitude subarctic and arctic biomes. On the skewed raw data a non-parametric Mann–Whitney U test found a significant difference between the medians of the high and low latitude biomes (family $U = 16$, $z = -2.101$, $p = 0.036$, dispersed band $U = 100$, $z = -5.896$, $p < 0.0001$, aggregated band $U = 106$, $z = -6.495$, $p < 0.0001$), with numbers of encounters being significantly lower in the high latitude biomes (family *median* = 37, *range* = 5–139, $N = 24$, dispersed band *median* = 7, *range* = 1–44, $N = 41$, aggregated band *median* = 3, *range* = 0–19, $N = 43$) compared to the lower latitude biomes (family *median* = 170, *range* = 39–292, $N = 4$, dispersed band *median* = 47, *range* = 11–219, $N = 29$, aggregated band *median* = 21, *range* = 4–75, $N = 35$). Parametric t-tests on the normalized $\log_{10}$-transformed data yield the same result.

4. Discussion

The gas model predictions suggest that maintaining contact across the tribe is not trivial, since random mobility cannot produce sufficient encounters to meet 1500 individuals face-to-face at most latitudes, barring equatorial aggregated bands. Hypothesis (i) can

thus be rejected: in general not all members of a tribe will not meet each other under the baseline assumption of random mobility. Furthermore, hypothesis (ii) can also be rejected because a significant negative relationship was found between absolute latitude and the predicted annual number of encounters regardless of the size of the basal mobile group (family, dispersed band or aggregated band). This suggests that if movement is random, higher mobility at high latitudes does not counteract the larger home range areas that have to be traversed.

In contrast, hypothesis (iii) cannot be rejected because the degree of reliance on hunting does show a significant negative partial relationship with predicted number of encounters, acting as an additive covariate with absolute latitude. Subsistence strategy and the associated spatial patterning and movement of the population thus seem to explain some of the variance shown in the number of encounters predicted for different societies inhabiting the same latitudes, at least under random mobility. The negative relationship between the percentage of the diet coming from hunted animals and the predicted annual encounter rate is probably due to the fact that groups relying more heavily on hunting require larger home ranges and these reduce the probability of randomly moving groups bumping into each other.

The gas model predictions were broadly similar for the family, dispersed band and aggregated band simulations. However, according to the gas model predictions, mobile aggregated bands, unlike the two smaller units, can maintain the tribe at low latitudes and the active network at high latitudes. Thus, contrary to the expectations from previous work (Grove et al., 2012), hunter–gatherers at higher latitudes might be *less* inclined to fission, so that they can more easily maintain their social networks. Overall, the gas model results indicate that hunter-gatherers do face a challenge in terms of maintaining tribal cohesion, which for the most part cannot be achieved through incidental inter-group encounters under random mobility.

To explore the limitations of random mobility as a means of maintaining social ties, the predicted number of encounters can be compared against the size of the different social network layers below the tribe (Figs. 4 and 5). The number of encounters predicted by the gas model implies that even if movement is random, contact could be maintained within an individual's entire active network (150-layer) at most latitudes, but perhaps not above ~70° latitude (Fig. 4). This may be why very few societies inhabit the regions nearest the poles. Furthermore, in contrast to lower latitude biomes, random movement fails to ensure encounters with all subgroups in the mating community (~500-layer) in the higher latitude subarctic and arctic biomes.

Fig. 4 suggests that the switch between sufficient and insufficient numbers of encounters to sustain the mating pool occurs at ~40° latitude for mobile bands. This accords well with the lower limit of the subarctic biome latitudinal range being at 45° latitude and the significant difference found between the number of encounters predicted for higher latitude subarctic/arctic biomes and lower latitude California/Mexico and desert/desert scrub biomes. It is interesting that it is at ~40° latitude that a switch also occurs from plant food making up 50 percent or more of the diet to animal products becoming the dominant component of the diet (Pearce et al., 2014), especially given the association between predicted annual encounter rate and reliance on hunting found here.

Since random mobility does not seem sufficient to maintain tribal cohesion through face-to-face contact and in addition cannot support mating pool cohesion at higher latitudes, future work can now legitimately explore the mechanisms by which social ties in these outer network layers are maintained in geographically dispersed networks. Since the results presented here suggest that network maintenance is a non-trivial concern for hunter-gatherers, the next step is to examine behaviours that either increase the rate of encounters between mobile groups or negate the need for frequent face-to-face interaction by providing the means of sustaining social ties remotely. These behaviours are expected to be particularly strongly expressed in environments in which random mobility fails to produce sufficient encounters for network maintenance, that is, where social cohesion is non-trivial. Since the hunter-gatherer gas model predicts that on the whole random mobility cannot sustain tribal cohesion, we should expect some strategies for facilitating network cohesion in all non-equatorial environments. However, at higher latitudes (above ~40°) random mobility cannot even maintain the mating pool, so additional strategies, perhaps especially cultural scaffolding, might be expected particularly at high latitudes. This would be exacerbated above 70° latitude, where it is predicted that members of randomly moving families and dispersed bands cannot maintain even their active networks.

Behaviours that promote inter-group encounters include frequent returns to home bases by band members and periodic aggregations of larger groupings. Indeed, home bases may partly have arisen in the first place in order to aid the cohesion of fissioned networks. Future work could use agent-based modelling, which has already yielded some surprising results in terms of the impact of mobility strategies on forager interactions (Premo, 2012), to examine the effect of coordinated mobility on social network connectivity in hunter-gatherers. Such models could also examine how network maintenance is affected by (i) fluid group composition, (ii) seasonal variation in mobility and fission-fusion associated with temporal and spatial resource fluctuations, and (ii) territoriality or home range sub-structuring, for example in terms of habitual hunting grounds, which would expand upon the modelling work of Wobst (Williams and Wobst, 1974; Wobst, 1974, 1976) by incorporating group movement.

If relationship maintenance cannot rely on frequent incidental face-to-face contact then cultural scaffolding of group cohesion and identity could allow relationships to be maintained *in absentia*. This may take the form of, for instance, group markers such as dialects (Cohen, 2012; Nettle and Dunbar, 1997) or ornamentation (Vanhaeren and d'Errico, 2006), extensions of kinship terminology and the associated obligations (Foley and Gamble, 2009), as well as the exchange of symbolic artefacts (Whallon, 2006; Wiessner, 2002), which provide an external memory aid for tracking the history of interpersonal interactions. Moreover, the ability to maintain indirect ties through third party gossip side-steps the need to interact with everyone face-to-face. However, these mechanisms may still rely on face-to-face interaction with some members of the wider network to some extent. For instance, seasonal aggregations of several bands are often used as opportunities to broker marriages (social ties) between members of different bands that habitually reside in distant areas, reinforce group affiliation through group rituals and music and facilitate reacquaintance between long-distance exchange partners (e.g. Guemple, 1971; Lee and DeVore, 1966).

According to the gas model presented here, cultural markers of tribal affiliation should be expected at all latitudes. However, in order to additionally connect members of a mating pool, markers identifying different mating pools within a single tribe are likely to be particularly pronounced, in terms of abundance and diversity, above ~45° latitude, the southernmost boundary of the Subarctic biome (Table 1). For instance, this might explain why we find heightened artistic expression in high latitude Europe during the later Pleistocene: contrary to widespread opinion (following McBrearty and Brooks, 2000) the Upper Palaeolithic ‘revolution’ may be a real phenomenon in Europe, associated with the emergence of cultural scaffolding to support network cohesion as

modern humans dispersed into higher latitudes and daily subsistence movement no longer ensured inter-group contact (Pearce, 2013). Although an explosion of artistic expression is commonly reported during the Gravettian, which is some time after the initial modern human dispersal into Europe, accumulating evidence suggests that such non-utilitarian artefacts are present from the earliest Upper Palaeolithic in Europe, at least in some regions (Conard, 2003, 2009; Higham et al., 2012; Kuhn and Stiner, 2007; Stiner et al., 2013). Furthermore, the fact that social bonding mechanisms that release individuals from proximate face-to-face interactions are expected specifically in the Subarctic/Continental Mid-latitude Forest biome might explain why the distribution of Aurignacian and Gravettian Venus figurines seems to occur predominantly in this biome at and above ~45° latitude, since it has been argued that such artefacts communicated group identity and were exchanged to bond large-scale networks (Gamble, 1982; Soffer et al., 2000; van Andel and Davies, 2003). Similar geographic patterns might be expected in artefacts purported to be personal ornaments, such as shell beads, as well as in the regional styles of tools. Additionally, the distances over which raw materials are transferred in different regions could potentially be used to infer the size of the social exchange networks that could be maintained as cohesive units in different areas.

In terms of the ethnographic record, we might expect stronger markers of group affiliation at higher latitudes, for example regarding styles of material culture and language that are shared by a tribe but demarcated at tribal boundaries. We might also predict kinship terminology that incorporates all members of a tribe rather than just close kin, and marriage rules that stress the importance of creating long-distance partnerships. In addition, we might expect a stronger emphasis on socially-constructed environments at higher latitudes, which could promote incidental meetings at certain meaningful points, such as ritual sites that require periodic visits, as described in Australia (Layton, 1986). Hypotheses like these, generated from models of hunter-gatherer interactions, can be readily tested once the empirical data become available.

Future models that simulate non-random movement of groups will provide more precise predictions regarding the expected geographic patterning of material culture in the ethnographic and archaeological record. However, the gas model predictions presented here are a crucial first step in determining whether maintaining tribal cohesion is so trivial that hunter-gatherers could achieve this even if they moved randomly around their home ranges. Since the gas model predicts that they could not, further work can now attempt to uncover the factors that are necessary for tribal maintenance in different environments.

5. Conclusions

The gas model presented here identifies environments in which maintaining face-to-face contact with members of different social layers is trivial, that is, can even be maintained when random mobility is assumed. More interestingly in terms of comparison with the archaeological and anthropological records, the null gas model also identifies environments in which random mobility would fail to produce sufficient face-to-face interactions between groups. The latter environments are where we would expect to find stronger evidence for behaviours that either increase the rate of inter-group encounters (such as recurrent visits to particular locations) or allow social bonds to be maintained without face-to-face interaction (such as exchange of symbolic artefacts). The hunter–gatherer gas model predicts that at lower latitudes contact across the entire mating pool of 500 individuals can be achieved even under random mobility, whereas at higher latitudes face-to-face interaction can only maintain layers up to the active network of 150 individuals. At higher latitudes, therefore, we should expect to see more marked evidence for non-random movement and/or cultural scaffolding of social network maintenance. However, the inability to sustain contact between all members of a tribe at most latitudes suggests that such behaviours should be found everywhere to some extent.

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